

THE SOUTHWESTERN WILLOW FLYCATCHER  
IN A GRAZED LANDSCAPE: MICRO-  
HABITAT AND PATCH-LEVEL EFFECTS  
ON THE RATE OF BROOD PARASITISM  
REPORT TO GILA NF

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IN A GRAZED LANDSCAPE:**



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ON THE RATE OF BROOD PARASITISM**

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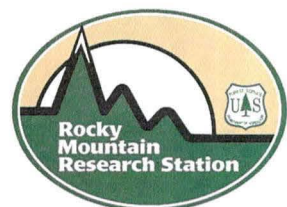
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This report is an outcome of a project developed and implemented in 1997 to monitor the large breeding population of the endangered southwestern willow flycatcher in the Cliff-Gila Valley. From 1997 to 2002, data collection and field work was directed by Dr. Scott Stoleson under the leadership of Dr. Deborah Finch. Scott Stoleson's contributions to this report are immeasurable. Scott currently holds a position with the USDA Northeastern Research Station in Pennsylvania but he constructed the study design and oversaw six years of quality data collection, on which much of this report is based. We would like to also thank him for valuable input and comments that improved this report.

The project represents the formation of partnerships between private and public entities. The project was first initiated by cooperation between the Phelps Dodge Mining Company and the Rocky Mountain Research Station with personnel from the Gila National Forest and Roland Shook of Western New Mexico University acting as mediators, working with us closely to ensure quality work and fair treatment of the land operation. The Gila National Forest and Phelps Dodge have contributed generous financial support that has allowed the project to continue in its work toward understanding the habitat requirements of the flycatcher that best contribute to productivity. Financial partners also include GeoMarine, Inc., the Nature Conservancy of New Mexico, the National Fish and Wildlife Foundation, and U.S. Fish and Wildlife. We would like to specifically thank Bruce Anderson, Paul Boucher, Jerry Monzingo, Ralph Pope, Art Talles, and Russell Ward of the Gila National Forest for the valuable support that has sustained the project since the inception; Ty Bays of Phelps Dodge for logistic and financial support; Dave Olgilvie, owner and operator of the U-Bar Ranch for assistance and land access; Gus Bodner, Paul Chan, Amanda Favis, Denise Friedrick, Joy Garcia, Brian Gibbons, Andrew Hagen, Dave Hawksworth, Rebecca Hunt, Michael Means, Giancarlo Sedoti, Allena Thompson, Bill Trussell, Hira Walker, Cynthia Wolf, and Hope Woodward for field assistance; and Rudy King for statistical guidance.

## INTRODUCTION

This document reports on the effects of brown-headed cowbird (*Molothrus ater*) brood parasitism on the endangered southwestern willow flycatcher (*Empidonax traillii eximus*). The data come from seven seasons of willow flycatcher nest monitoring along the Gila River in southwest New Mexico. The primary goal of this project has been to determine levels of nest success, cowbird parasitism and predation rates for the southwestern willow flycatcher and to characterize and quantify the habitat at nest sites. The main objectives of the analyses conducted for this report were to quantify levels of brood parasitism on this population of willow flycatcher and discern habitat and landscape characteristics that may be associated with higher levels of parasitism. Brown-headed cowbirds associate with cattle so we were particularly interested to know if the distance to summer grazing would influence the rate of brood parasitism. Because there have been conflicting reports of “edge effects”, we wanted to determine if the distance of the nest to the edge of the patch had an influence on the rate of brood parasitism. We were also interested in the influence of patch size on parasitism to determine if smaller patches are more accessible to a breeding cowbird. Additionally, because the southwestern subspecies of the willow flycatcher is associated with saturated soils, we were interested to see if the distance to different water sources would influence the rate of brood parasitism.

We report on rates of brood parasitism each year, and on factors influencing rates of brood parasitism. Using logistic regression, we examined the potential impacts of microhabitat at the nest site, patch structure, distance to summer grazing, patch edge, active floodplain, and water. The report concludes with a discussion of the results in the context of other research results.

## BACKGROUND

### THE SOUTHWESTERN WILLOW FLYCATCHER

The southwestern willow flycatcher is a small songbird that migrates to the southwestern United States to breed in dense riparian vegetation along river corridors. The



southwestern willow flycatcher, one of four recognized subspecies of *E. traillii*, was federally listed as endangered in 1995, and is state listed as endangered in California, New Mexico and Utah, and as a Species of Special Concern in Arizona (U.S. Fish and Wildlife Service (USFWS) 2002, Biota Information System of New Mexico (BISON)). It is currently considered the top priority species for US Fish and Wildlife Service Region 2. The most current count estimates the total number to be approximately 1,000 breeding pairs (USFWS 2002, Sogge *et al.* 2003). Declines have been attributed primarily to a loss and alteration of riparian habitat associated with anthropomorphic influence on floodplains, including grazing, and resulting in a reduction of water levels and degraded habitat (USFWS 2002). Negative effects of brood parasitism on breeding productivity have also been listed as a threat to flycatcher (Stoleson and Marshall 2000, USFWS 2002).

#### **THE BROWN-HEADED COWBIRD**

The brown-headed cowbird is a generalist, obligate brood parasite whose range has expanded dramatically in recent history (Lowther 1993). Originally limited to short-grass prairie, the cowbird foraged behind bison, feeding on the insects stirred up by the herd (Lowther 1993, Robinson *et al.* 1995). The cowbird expanded its range as European settlement changed the landscape; as forests were fragmented from logging and much of the land was converted or cleared for grazing and farming (Lowther 1993, Robinson *et al.* 1995, Schweitzer *et al.* 1998). The landscape changes promoted the expansion of cowbirds, as they were able to forage with livestock and have access to the nests of breeding birds in the adjacent forests. The cowbird's range expanded westward as arid landscapes were converted to farmland and rangeland (Robinson *et al.* 1995).

In the Southwest, cowbirds were documented as present as early as 1858 but apparently they did not begin increasing until the late 1800s (Whitfield and Sogge 1999). Analysis of early museum collections of willow flycatcher nests in the Southwest did not show any evidence of brood parasitism in the late-1800s but a nest collected in 1900 near Yuma, Arizona contained the first documented cowbird egg in a southwestern willow flycatcher nest (Whitfield and Sogge 1999). Over the last century, the cowbird population has

grown and the rate of brood parasitism has correspondingly increased (Schweitzer et al. 1998, Whitfield and Sogge 1999). Breeding Bird Survey data show the cowbird population in New Mexico to be on a slightly positive trend (nonsignificant) (0.2% per year) from 1966-2002 but analysis of more recent data (1980-2002) suggests cowbird numbers may be currently declining in New Mexico (-1.8% per year) (nonsignificant) (Sauer et al. 2003).

Breeding cowbirds are most abundant in riparian areas and other areas with a high density of host species (Tewksbury et al. 1999). Floodplain landscapes have been significantly altered by human development through clearing, grazing, construction, industrial development, and river control (Periman and Kelly 2000). Human disturbance is a common characteristic of cowbird habitat, which is best described as having wood-field ecotones rather than extensive woods or treeless grasslands (Lowther 1993). Riparian zones, especially the naturally fragmented and narrow zones of the West, form sharply contrasting ecotones with the surrounding landscape. In the Bitterroot Valley of western Montana, cowbird abundance was greatest in riparian habitats within 2 km of agricultural areas (Tewksbury et al. 1999). Riparian zones are highly productive and support a high abundance and diversity of breeding birds (Hubbard 1971, Knopf et al. 1988). The proximity to open pasture and agriculture and opportunity for breeding riparian habitat with a high density of breeding birds make the floodplains highly suitable for the cowbird during the breeding season.

#### **IMPACTS OF COWBIRD PARASITISM**

Brood parasitism reduces a host's productivity in a variety of ways. Commonly, a cowbird will remove a single host egg after laying (Lowther 1993). The effects of brood parasitism are more detrimental to small birds, which often fail to raise their own young if the cowbird egg hatches (Robinson et al. 1995). Cowbird eggs hatch in 9-10 days (Lowther 1992), shorter than the length of incubation for most species. The cowbird nestling is naturally larger than the smaller host is, it will hatch out earlier, and it will successfully outcompete its nestmate for food. Studies on feeding rates demonstrate that parents will feed cowbirds at a higher rate than their own young (Lowther 1992,



Dearborn 1999). Cowbirds also beg louder and more frequently than host young, which may also increase the risk of nest predation (Dearborn 1999). There have also been reports of more destructive behaviors by the cowbird such as destruction of eggs (Scott et al. 1992, Sealy 1994, Pietz and Granfors 2000) and even nestlings (Brown 1993, Scott and McKinney 1994, Grzybowski 1995, Sheppard 1996, Elliott 1999, Woodward and Stoleson 2002, Igl 2003), although these behaviors are not common.

Reproductive costs associated with brood parasitism are often implicated as a major contributor to the declines of many vulnerable species. Particularly high rates of brood parasitism have been documented for a number of vireo species (Ward and Smith 2000, Ortega and Ortega 2003) including the endangered black-capped vireo (Grzybowski 1995), and least Bell's vireo (Brown 1993). The extreme decline of the Kirtland's warbler was exacerbated by high rates of brood parasitism (Lowther 1992, Mayfield 1992). Brood parasitism is cited as a factor contributing to the decline of the southwestern willow flycatcher (Whitfield and Sogge 1999). Cowbirds do not specialize in one species, and so can be potentially hazardous to threatened species because the brood parasitism rate will not decline in response to a lowered population density (Rothstein 1975, Pease and Grzybowski 1995).

Brood parasitism limits nesting success but does not always impact population levels. Population modeling has shown that nest predation has a greater impact on seasonal fecundity than brood parasitism does (Pease and Grzybowski 1995, Schmidt and Whelan 1999). Rates of brood parasitism on individual nests do not take into account the outcome of subsequent nest attempts and therefore will inflate the effect on reproductive productivity (Pease and Grzybowski 1995, Schmidt and Whelan 1999). Further, not all parent birds are equally vulnerable to parasitism. In a study of hooded warblers (*Wilsonia citrina*) breeding in forest fragments, intensive cowbird trapping decreased the average parasitism rate from >50% to 9%, but had no effect on average nest success. This apparent paradox probably was because those nests most likely to be parasitized (those of inexperienced parents) were also those most likely to be depredated (Stutchbury 1997).

### FACTORS AFFECTING THE RATE OF BROOD PARASITISM

Several factors have been reported as contributing to the rate of brood parasitism including proximity to open habitat, nesting habitat, and cowbird abundance. However, results vary among locations, species, and habitats; patterns aren't always predictable; and conflicting evidence can be found for many factors (Hahn and Hatfield 1995). There is some evidence that cowbird abundance declines as the distance to the edge of the habitat increases (Brittingham and Temple 1983). Other studies, however, have not found that parasitism is higher near the forest edge (Hahn and Hatfield 1995, Tewksbury et al. 1998). The structure and floristics of breeding habitat at the nest site and the position of the nest within the habitat may have an effect on the brood parasitism rate (Robinson et al. 1995). Burhans (1997) found nest concealment to be associated with a lower parasitism rate, but the correlation only held in one type of habitat and for only one avian species. Acadian flycatcher nests (*Empidonax vireescens*) were more likely to be parasitized in habitat with a more open subcanopy and canopy (Brittingham and Temple 1996). Wilson and Cooper (1998) found that for Acadian flycatchers, higher nests were associated with lower parasitism rates. Hahn and Hatfield (1995) reported that low-nesting species were more likely to be parasitized than mid- to high-nesting species.

High cowbird abundance is associated with both high host densities and the presence of grazing or other feeding sources. High host density is predictive of cowbird abundance (Robinson et al. 1995, Tewksbury et al. 1998, Tewksbury et al. 1999). Riparian areas support high densities of breeding birds (Sanders and Edge 1998) and in areas where cowbirds are already abundant, breeding activities are often concentrated in the deciduous riparian zones (Tewksbury et al. 1999). High cowbird abundance is also tied to the presence of feeding sources, both grazing and human-based sources. There is evidence that cowbird abundance and rates of brood parasitism increase with proximity to grazing (Robinson et al. 1995, Morse and Robinson 1999, Goguen and Mathews 1999, Goguen and Mathews 2000). Agricultural landscapes are strong predictors of cowbird abundance (Gates and Evans 1998, Stribley and Haufler 1999, Tewksbury et al. 1999, Young and Hutto 1999). Although cowbirds congregate around food sources, they can



commute up to 7 km between breeding and foraging areas (Rothstein et al. 1984) so removing cattle from the immediate area does not preclude brood parasitism. In Colfax County in northeastern New Mexico, Goguen and Mathews (2000) found cowbirds will increase commuting distances from grazed areas to breed and found a parasitized nest greater than 8 km from grazing. Kostecke et al. (2003) radiotracked female cowbirds and found they were commuting longer distances between foraging and breeding sites after the reduction of stocking rates in the vicinity. They also found that although the females were commuting larger distances, parasitism rates were recorded as 13 times lower after the stocking rate reduction.

### **BROOD PARASITISM AND ITS EFFECTS ON WILLOW FLYCATCHERS**

Brood parasitism by the brown-headed cowbird has been identified as a threat to the flycatcher (Robinson et al. 1995, Marshall and Stoleson 2000, USFWS 2002). Before the flycatcher was listed, Unitt (1987) recognized that although brood parasitism may have played a part in the decline of the subspecies, the contribution was unknown. Subsequent listing of the subspecies prompted intensified research on the flycatcher and although the role parasitism currently plays on population reproductivity is still not clear, the consensus has shifted and much of the literature supports the idea that cowbird parasitism may not be a primary threat to larger populations as long as adequate habitat is available and productivity rates are high enough to offset any adverse effects (Sedgwick and Iko 1999, USFWS 2002, Rothstein et al. 2003).

The effect of brood parasitism on the reproductive rate of willow flycatchers is highly variable (Rothstein et al. 2003). Actual parasitism rates vary among sites and years, ranging from 3-66% (USFWS 2002). Cain et al. (2003) reported a low rate of brood parasitism on willow flycatcher in the Sierra Nevada of California where the major cause of nest failure was predation. Sedgwick and Knopf (1988) followed breeding willow flycatchers throughout the season and concluded the impact of brood parasitism was greater if measured as single nest productivity rather than as seasonal fecundity. From a long-term study on the effects of brood parasitism on the population dynamics of a willow flycatcher population in Oregon, Sedgwick and Iko (1999) concluded that

predation exerts a greater selective pressure than parasitism. At the Kern River Preserve, where a cowbird-trapping program was used to reduce the impacts of brood parasitism, the willow flycatcher population did not respond favorably to the lowered parasitism rates (Whitfield et al. 1999). Limiting factors are more likely to be deficiencies in quality breeding habitat and factors on migration and wintering grounds (USFWS 2002, Rothstein et al. 2003).

Brood parasitism reduces the individual nest success of the willow flycatcher but direct effects on the population are difficult to assess. Willow flycatchers do not usually fledge their own young when they are parasitized (Sedgwick and Iko 1999, Whitfield and Sogge 1999, Rothstein et al. 2003). Whitfield and Sogge (1999) found that fewer than 2% of nests fledging a cowbird also successfully fledged a flycatcher. Like the majority of cowbird hosts, the willow flycatcher is categorized as an “acceptor” species and shows no recognition of the presence of a cowbird egg in its nest. However, *E. t. extimus* will desert approximately 35-75% of parasitized nests and reneest (Rothstein et al. 2003). This behavior improves the likelihood of an individual successfully fledging young during the season, and has been viewed by some as a general defensive response to parasitism (Parker 1999). The impact of brood parasitism is therefore difficult to assess from a proportion of individual nesting attempts that are parasitized. Measures of simple nest success may actually inflate the impacts of brood parasitism because it does not take into consideration the potential for fledging young in subsequent nesting attempts (Pease and Gryzbowski 1995, Schmidt and Whelan 1999). Renesting behavior increases fecundity, but there is still a cost paid for the extra time spent attending nests, building more nests, laying more eggs, and fledging young later in the season (Sedgwick 2000). Overall, parasitism has been shown to reduce the number of offspring raised in the season (Sedgwick and Iko 1999).

The southwestern willow flycatcher is a late breeder for a passerine species (Sedgwick 2000) and timing of nesting may be related to threats of parasitism (Ellison 1999, USFWS 2002). Early nests are potentially more productive, and because the flycatcher begins breeding when many other species are past the incubation stage, they may



experience higher levels of parasitism earlier in the season, which could have greater impacts on seasonal productivity (USFWS 2002, Rothstein et al. 2003).

## METHODS

### STUDY SITE

The Cliff-Gila Valley opens onto a broad alluvial floodplain as the river leaves the mountains of the Gila Wilderness. The upstream end of this wide valley begins at the Mogollon Creek inlet (33° 55' N, 108° 35' W) and from here the river runs south-southwest through the Cliff-Gila Valley for approximately 18 km (Figure 1 and 2). Elevations range from 1350 to 1420 m. Most of the Cliff-Gila Valley consists of irrigated and non-irrigated pastures used for livestock and hay farming. The riparian patches support one of the highest densities of non-colonial breeding birds in the United States (Stoleson and Finch 1997, Stoleson and Finch 2000). High breeding bird densities in riparian woodlands in a matrix of pastureland and farmland is characteristic of the wood-field ecotones that the BHCO prefers (Lowther 1993, Tewksbury et al. 1999, Young and Hutto 1999). Riparian patches on floodplain terraces are characterized by a mature Fremont cottonwood (*Populus fremontii*) overstory with a subcanopy dominated by stands of boxelder (*Acer negundo*) and Goodding's willow (*Salix gooddingii*). In many stands, the boxelder is the most common tree, forming a closed subcanopy gallery forest. Most young patches support a Fremont Cottonwood-Goodding Willow community type (Muldavin et al. 2000). This community is typically found on low to mid-elevation bars within the active floodplain.

The Gila River Bird Area (GRBA) is located along approximately 5 km of the Gila River at the north end of the Big Burro Mountains (Figure 1). Elevations range from 1,345-1,315 m (4,415-4,310 ft.) The GRBA is on public land administered by National Forest. Grazing at the site is limited to the dormant season. Adjacent to the river, the floodplain supports a forested wetland community dominated by Fremont's Cottonwood and Goodding's Willow. Coyote Willow dominates the understory and forms monotypic linear patches lining the river. Boxelder and early-succession Seepwillow (*Baccharis glutinosa*, *B. emoryi*) are a minor component of the habitat.

**Figure 1.** Study site map.

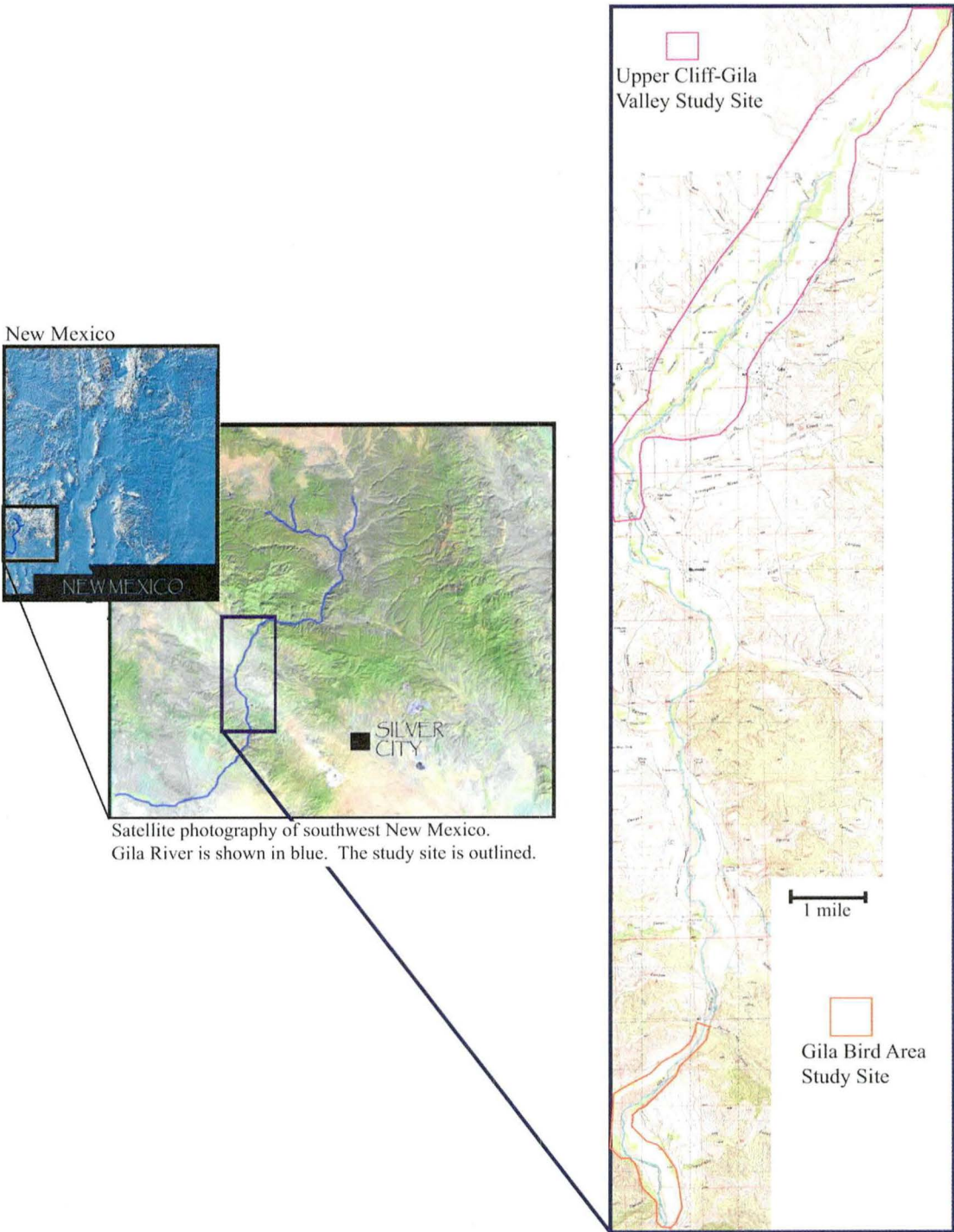
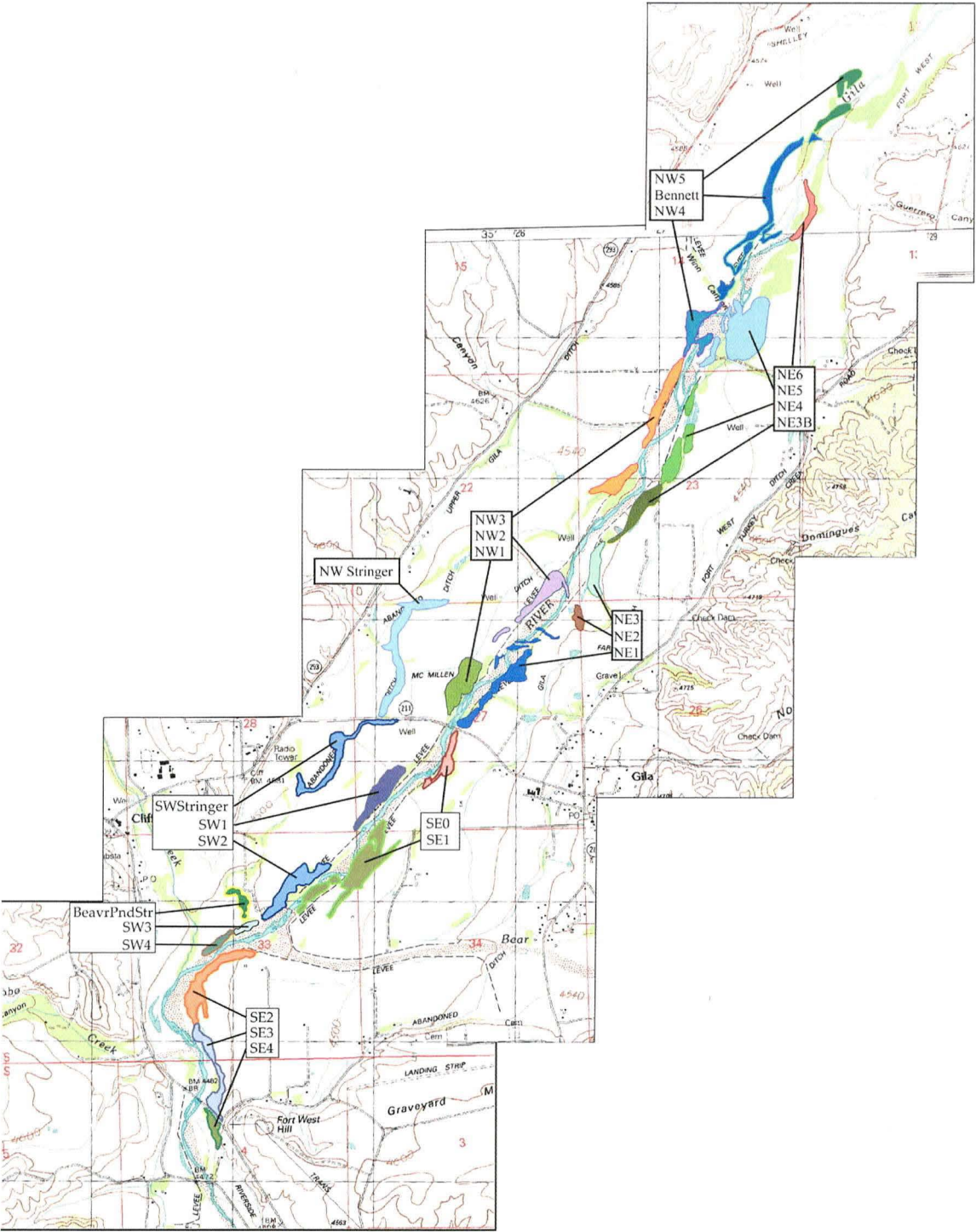


Figure 2. Riparian patches in the Cliff-Gila Valley.





## **NEST MONITORING**

Data on nesting activities were collected every year from 1997 to 2003 from mid-May to the end of August. We conducted nest searches on a daily basis and nests were monitored every 3 – 7 days following a modification of Rourke et al. (1999). Flycatcher behavior, nest activity and nest contents were recorded on each visit. For nests below 5 – 6 meters, nest contents were observed with pole-mounted mirrors or video cameras to ascertain nest stage and presence/absence of cowbird eggs or chicks. Because it is difficult to handle the poles above 5 – 6 meters, high nests were monitored with binoculars from a distance and contents determined from adult activity at the nest. We used all necessary precautions to minimize human-impacts when conducting nest search and monitoring activities (Martin and Geupel 1993, Martin et al. 1997, Rourke et al. 1999). We recorded presence or absence of brood parasitism for all nests where it was possible to observe the nest contents. Brood parasitism rates were calculated as the number of nests that were confirmed as parasitized divided by the number of nests with known parasitism status.

## **HABITAT SAMPLING**

We sampled habitat characteristics at each nest site at the end of each season after the flycatchers had vacated the territories. For each nest, we recorded the height of the nest tree, the height of the nest, the tree species used as substrate, and the diameter of the nest-tree trunk at breast height (DBH). UTM-coordinates for each nest were recorded using Garmin GPS-12.

## **LANDSCAPE CALCULATIONS**

We used GIS software to project nest locations, delineate riparian patches, and calculate distances to grazing and other floodplain features. Brown-headed cowbirds associate with cattle so we were particularly interested to know if the distance to summer grazing would influence the rate of brood parasitism. Because there have been conflicting reports of “edge effects”, we wanted to determine if the distance of the nest to the edge of the patch had an influence on the rate of brood parasitism. We were also interested in the influence of patch size, hypothesizing that smaller patches would be more accessible to a

breeding cowbird. Additionally, because the southwestern subspecies of the willow flycatcher is associated with saturated soils, we were interested to see if the distance to different water sources would influence the rate of brood parasitism. We used the Spatial Analyst extension in ArcView 8.2 to calculate distance grids to active summer grazing, edge of the riparian patch, stagnant water, and the active floodplain. We did not consider distance to the spatially dynamic river and instead calculated the distance to the active floodplain because the water table is either exposed or very near to the surface across the entire landform (Keddy 1999). UTM nest locations were projected over USGS Digital Orthoquads in ArcView and the projected locations were reviewed for accuracy. We used an avenue extension GridPig v2.6 (Hare 2003) in ArcView 3.2 to acquire the value of each calculated distance grid at each GPS nest location. We calculated the area of each habitat patch and joined the results to the nest attributes.

## DATA ANALYSIS

We used SPSS, v. 10.1 statistical program to analyze the data. To explore the data we compared the differences between parasitized and unparasitized nests by reviewing mean values, variance values, and boxplots for each variable. We used each variable as a predictor in logistic regression to test for differences in parasitism status using presence or absence of parasitism as the dependant variable. To visualize each relationship, we constructed scatterplots with the mean parasitism rate on one axis and incremental combinations of each variable on the other. Each variable was run independently to test the significance of any influence on the rate of brood parasitism. We used a likelihood ratio test statistic to assess the significance of each single variable. We then entered all variables in stepwise variable selection for model building. Likelihood ratios were used to determine variable entry and removal. We used probability criteria of 0.05 for parameter entry and 0.1 for removal. The Hosmer-Lemeshow test was used to check the model's agreement with the observed data. The odds-ratio was used to interpret the influence of each predictor in the model. The odds-ratio is the ratio of the estimated odds of occurrence before and after one incremental increase in the predictor. It is easily calculated by taking the base of the natural logarithm raised to the power of the estimated

regression coefficient (Neter et al. 1996). We also reviewed boxplots of predicted probabilities and residuals to check how well the model predicts the data.

## RESULTS

### NOTEWORTHY OBSERVATIONS

We recorded three rare occurrences of a flycatcher and a cowbird successfully fledging from the same nest. The first case was recorded in the Northwest Stringer in 1998. An observer witnessed a cowbird fledging and recorded the parents as actively feeding two older, active flycatcher nestlings, approximately 2 - 4 days before their estimated fledging date. The observer reported that the adults were flying past the cowbird fledgling to take food to the nest, “even though (the cowbird) was begging loudly”. We recorded two additional occurrences in 2003. The first was recorded in Southwest-1 during July. We observed the cowbird fledging on July 29<sup>th</sup>, while a fully feathered flycatcher nestling remained in the nest. We returned on August 1<sup>st</sup> to find the flycatcher had fledged and that the parents were still actively feeding both fledglings. The flycatcher fledgling was still present and begging from the parents on August 4<sup>th</sup>. The second instance was recorded in Northwest-1 during August 2003. On August 11<sup>th</sup>, a cowbird fledged from a nest that still contained a flycatcher nestling. On August 14<sup>th</sup>, an observer recorded the parents feeding both the cowbird and the flycatcher, which had since fledged from the nest. This incident was a second brood. The cowbird and flycatcher were raised in the same nest that had successfully fledged at least one flycatcher on July 10<sup>th</sup>, 2003.

### BROOD PARASITISM RATE

We calculated the rate of brood parasitism by year and by patch (Table 1). The total rate of brood parasitism across all years and for all locations was 20.3%. This rate was estimated from 472 nests with confirmed presence or absence of parasitism. But an additional 419 nests were either too high to inspect contents or the nest was deconstructed and used for rebuilding in a new location before we were able to confirm cowbird activity. Our reported rate of brood parasitism may be slightly inflated because the nests that weren't inspected were generally the high nests and we found that high nests in boxelder had a lower probability of being parasitized (*see Section on Habitat below*).



The rate of parasitism in each year varied from a low of 11.1% in 1997 to a high of 31.4% in 1998.

The rate of brood parasitism by patch varied widely from 0 to 100%, but when patches with fewer than 5 observations were removed the maximum rate changed to 66.7%. Chi-squared tests were performed to check if the observed rates of brood parasitism for each patch fell significantly below or above the expected rate. Southeast 1, Northeast 1, and Northeast 5 had significantly higher parasitism rates than were expected (Table 2).

### **HABITAT CHARACTERISTICS**

Nest tree measurements were evaluated for any relationship between nest-site characteristics and the rate of brood parasitism. All nests with a known parasitism status were used in the analyses.

*Tree Species* – The rate of brood parasitism did not significantly differ among the different tree species. Chi-squared tests were used to test whether the species of tree used as nest substrate significantly affected the chance of a nest being parasitized. Nests built in boxelder and cottonwood had a lower rate than expected but it was not found to be significantly different than the overall proportion. All species other than boxelder and cottonwood had higher than expected rates, but the differences were not significant.

*Tree Characteristics and Nest Height* – In general, nests in taller boxelder substrates and higher nests in boxelders were less likely to be parasitized. Habitat variables used in analysis included: nest height, tree height, tree-trunk diameter at breast height (DBH), and relative position of the nest in the tree measured as a proportion of nest height to tree height.

To test the differences in the means between parasitized and non-parasitized nests for all tree species combined, we explored the data using one-way ANOVA. The data for each variable were normally distributed. Nests that had not been parasitized were built in

taller trees, with larger trunks, and they were built higher in the tree – for both absolute distances from the ground and for proportion of tree height.

Tree structure varies greatly by species so we analyzed each tree species separately to determine if the same conditions held true for each. We found that these relationships were primarily true only for boxelder, except for proportional height, which was higher for non-parasitized nests in all species (Table 3). Comparable to boxelder, non-parasitized nests in Arizona alder were built significantly higher and built in taller trees with significantly greater DBH. Tree species other than boxelder and alder that the flycatcher commonly nests in include Goodding's willow, seepwillow, and young cottonwood. When comparing the means of parasitized and non-parasitized nests in these species the trend reverses: the greater heights and trunk diameters are in trees that were parasitized, although few of these differences were statistically significant ( $\alpha < 0.01$ ). The structure of these tree species at the stage when they are used as nesting substrate by the flycatcher can be described as being shorter with thin trunks typically less than 10 cm in diameter. The only significant difference between the height and diameter variables for these shorter, small-stemmed tree species was that the mean seepwillow height was significantly higher for parasitized nests than for trees with unparasitized nests. Seepwillow is an early-succession species with very rapid growth and short life span. Smaller trees of seepwillow, young cottonwood, and willow species (*Salix spp.*) may be more likely to have taller trees over them, thereby providing greater concealment for nests.

We used logistic regression with each variable as a single predictor to further describe its relationship with the rate of brood parasitism. The significance of each univariate analysis was similar to the ANOVA output (Table 4). The estimated regression coefficient in the analysis with nest height as the single predictor indicates that the odds of parasitism occurring decrease by approximately 25% with every one meter increase in nest height. Analysis with tree height as the single predictor ( $b = -0.0876$ ,  $p = 0.001$ ) indicates that the odds of parasitism occurring decrease by approximately 10% for every one meter increase in tree height. Similarly an increase of one cm DBH, decreases the

odds of parasitism by approximately 5% ( $p < 0.001$ ) and an increase of 1% of the proportion of the nest height to tree height decreases the probability of parasitism by 9% (e.g., when the nest height increases from 50% of the tree height to 51% of the tree height).

#### LANDSCAPE-LEVEL CHARACTERISTICS

*Patch Size* – The probability of brood parasitism increased with larger patch size ( $p = 0.001$ , likelihood ratio test) (Table 4). The patches identified as having greater rates of brood parasitism (see Brood Parasitism Rate section above) all had relatively high patch areas, ranking first, second and seventh in patch area ( $n=25$ ). The relationship between probability of parasitism and patch area may explain the high rates in those patches.

*Distance to Grazing* - The mean distance to grazing was lower for parasitized nests but the likelihood ratio test obtained from univariate binomial regression showed the variable did not significantly improve the performance of the null model ( $p = 0.266$ ) (Table 4). We used a chi-squared test to further investigate any influence grazing may have had on brood parasitism rates. We found no significant difference in brood parasitism rates between patches that were far removed from summer grazing (Gila Bird Area, Fort West Ditch site, and The Nature Conservancy) and those on or adjacent to the U-Bar Ranch ( $p = 0.82$ ). Additionally, there was not a significant difference between the observed and expected frequency of brood parasitism in Gila River Bird Area, which is even further removed, compared with all data in the Cliff-Gila Valley ( $p = 0.41$ ,  $n_{GBA} = 10$ )

*Distance to Stagnant Water* – Nests built closer to stagnant water were more likely to be parasitized ( $p = 0.028$ , likelihood ratio test) (Table 4). Standing water is present both from pooling of irrigation run-off and in discontinued river channels, backwater channels, and oxbows. The availability of water allows for regeneration of mesic riparian habitat. Dense riparian habitat in turn attracts many breeding birds because of the number of concealed nest sites available. These areas with high-host densities may be attracting breeding cowbirds in the same manner as the larger patches. Some of the other stagnant water sources are discontinued channels on the floodplains. These habitats tend to be



younger cottonwood/willow patches, on gravel bars distinct from the main patches, and are very limited in size. These types of patches are typical of flycatcher breeding habitat in two of the patches that were found to have higher than expected rates of brood parasitism, Northeast-1 and Northeast-5. Nests in these patches were not as well concealed and were easier to find (personal experience), which may result in greater levels of brood parasitism.

### TIME OF SEASON

We found the mean date of nests that were parasitized was 4 days lower (June 26 +/- 19.2 days) than the mean date of nests that were not parasitized (June 30 +/- 17.7 days). This relationship was not found to be statistically significant using one-way ANOVA, nor did the date have any influence on the odds of being parasitized ( $p = 0.234$ , likelihood ratio test).

### MULTIVARIATE PARASITISM MODEL

The final model chosen using both forward-stepping and backward-stepping binomial regression retained the variables: nest height, distance to edge, and patch area (Table 5).

$$\text{OddsBP} = -1.1461 - 0.1509 * \text{NestHt} - 0.0221 * \text{Dedge} + 0.1384 * \text{PatchArea}$$

These three variables had the greatest influence on the odds of parasitism. Interpretation of the log-odds gives tangible reference as to the influence of each variable, while the other variables are held constant. The odds of a nest being parasitized declined by approximately 16% with each 1-meter increase in nest height. The odds of parasitism declined by 2% with every 1-meter step into the interior of the patch. The odds of parasitism increased by 14% as patch size increased by 1-hectare. Although the purpose of model building in this analysis was to identify key explanatory values, the model is moderately reliable as a predictor.

## DISCUSSION

### THE RATE OF BROOD PARASITISM

The average rate of brood parasitism for willow flycatchers in the Cliff-Gila Valley and the Gila Bird Area fell below the average rate for the subspecies. Using data from

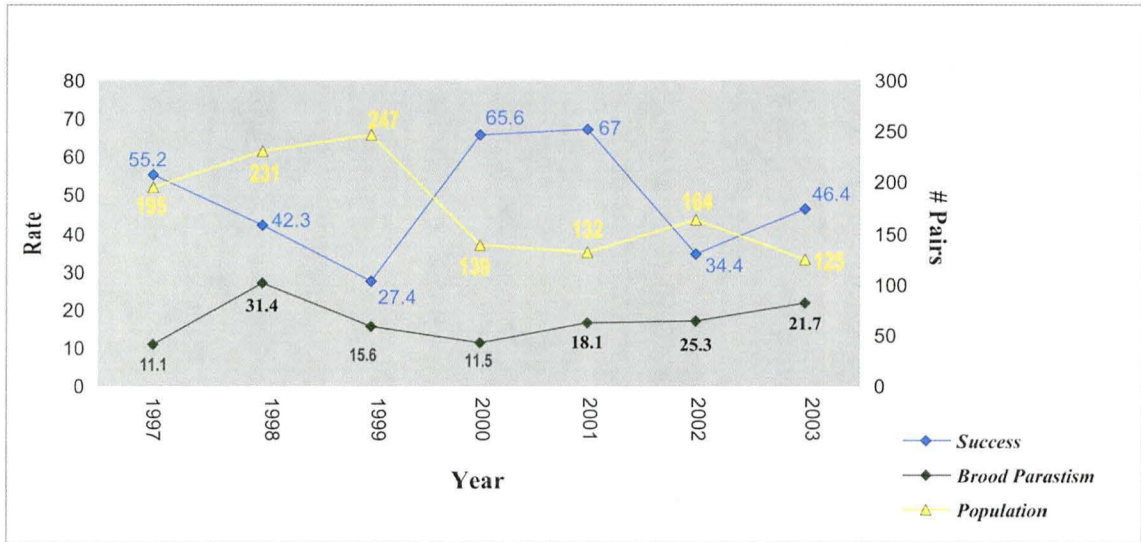
Rothstein et al. (2003) we looked at the brood parasitism rate of 12 sites in the Southwest and compared them with our data. The average rate of 20.3% at our sites was lower than the 28% mean for the reported populations. We also used the data from Rothstein et al. (2003) to calculate expected values from the proportion parasitized in the Southwest. Using chi-squared tests, we determined the expected number of parasitized nests was significantly higher than what we observed ( $p < 0.001$ ). The rate of brood parasitism for the population on the South Fork of the Kern River, California was extremely high (66%) and was influential in the expected value calculation. When data from the Kern River Preserve were removed from the overall pool of data, the data from our study were consistent with those expected from the data pool.

The rate we calculated in this study was the rate of brood parasitism per individual nests. Rates of brood parasitism on individual nests do not take into account the outcome of re-nest attempts by the same pair and therefore may overestimate the negative impact of parasitism on seasonal fecundity and the population growth rate (Pease and Grzybowski 1995, Schmidt and Whelan 1999). In 2003, we followed subsequent nest attempts to get an estimate of territory productivity. Nests that were located near ( $<15\text{m}$ ) to a previously active nest (often in the same tree), and whose dates of activity did not overlap the preceding nest, were documented as re-nests. Observations of flycatcher activity, such as removing material from the inactive nest and using it to rebuild a new nest, often helped to confirm the status of a new nest as a re-nest. We recorded multiple nesting in 34 territories. Second-broods were attempted in nine territories, four of which were successful (Brodhead and Finch 2003). Per-territory success was estimated at 66.3% while individual nest success was 46.4%.

The number of breeding flycatchers in this population dropped substantially from a high of 247 pairs in 1999 to 125 pairs in 2003 (Figure 3). Climate, specifically drought, may have been partially responsible for the decline (Stoleson and Finch 2000, Brodhead et al. 2002, Brodhead and Finch 2003). Density-dependent factors may also have been responsible for a low rate of nesting success in 1999 (Stoleson and Finch 2000). Data up through 2001 show a negative density-dependent relationship of nest success with lower

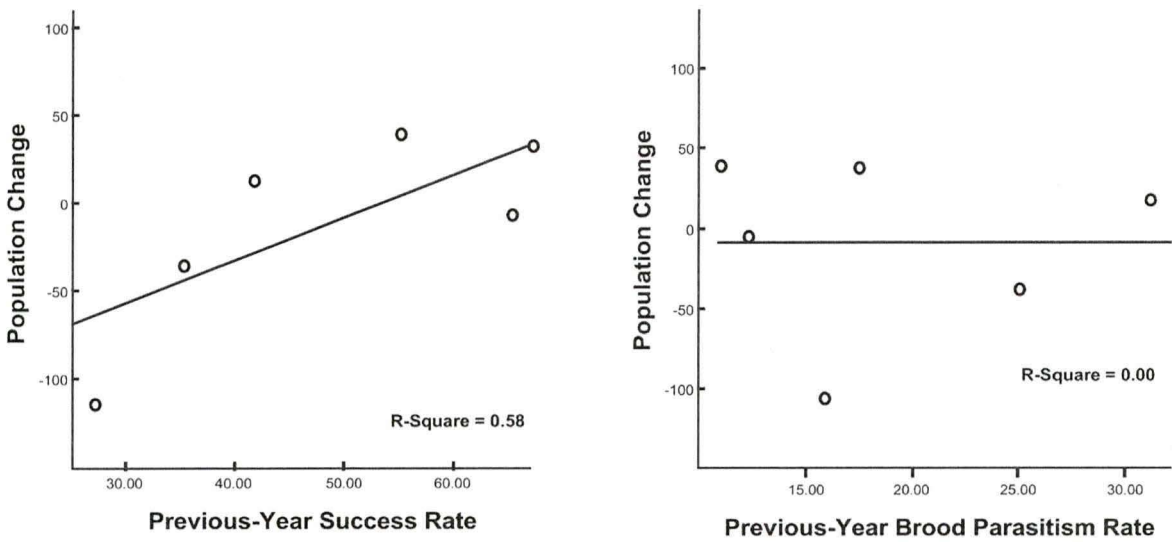
overall nest success in seasons with a larger breeding population. If low nest success had an effect on the population size, it is more likely that predation had a greater impact than brood parasitism. Population modeling has shown that nest predation has a greater impact on seasonal fecundity of songbirds than brood parasitism (Pease and Grzybowski 1995, Schmidt and Whelan 1999). Most nest failures in this population result from predation (Stoleson and Finch 1999). Given that the two drops in population were preceded by low nesting success rates the previous year (Figure 3), it is conceivable that the number of returning flycatchers is related to the previous year’s success rate. Testing this observation, we found the change in population size from one year to the next was correlated with prior-year nest success ( $r^2 = 0.76$ ) (Figure 4). We did not find any correlation between the change in population size and the brood parasitism rate ( $r^2 = 0.000$ ) (Figure 4).

**Figure 3.** Population size, brood parasitism rate, and nest success rate for each year.





**Figure 4:** Association of success rate with the subsequent year’s population size.



**PRODUCTIVE HABITAT**

Logistic regression modeling indicated that larger patches are more likely to have higher rates of parasitism, and that greater distance to the patch-edge and greater nest height reduce the likelihood of parasitism. Other reports provide similar evidence. Burhans and Thompson (1999) found that yellow-breasted chat nests in larger patches were more likely to be parasitized. Wilson and Cooper (1998) found that for Acadian flycatchers, higher nests were associated with lower parasitism rates. Hahn and Hatfield (1995) reported that low-nesting species were more likely to be parasitized than mid- to high-nesting species.

Reports on edge effects on parasitism levels vary tremendously. Similar to our study, Brittingham and Temple (1983) showed that cowbird frequencies declined as the distance to the edge of the habitat increased. Morse and Robinson (1999) found that parasitism levels declined with increasing distance from agricultural edge but they did not find the relationship to be true with other edge types. Contrary to what we found, Burhans and Thompson (1999) found that nests further from the edge were more susceptible to parasitism. However, they defined the patch as “interlocking leafy vegetation” and we

defined patch as continuous riparian habitat bounded on all sides by another landcover type, and measured to where the habitat changed to an open field or gravel bar.

Variation in habitat type is important to consider when comparing results. Donovan et al. (1997) found that the detection of edge effects varied in their study area depending on landscape type. None of the reports on edge effects on the rate of brood parasitism that we reviewed were from studies in riparian habitat in the Southwest. Distinct from extensive broad-leaved forests elsewhere, riparian habitat in the Southwest is naturally limited in size, narrow, and linear. The patches are relatively small at our study site, with the largest patch measuring 11.8 hectares and the greatest distance to edge measuring 65.3 meters. Paton (1994) reviewed research reporting on edge effects on both predation and brood parasitism. He alleged that studies reporting on edge effects within 50 meters from the patch-edge were most convincing and suggested that research designed to detect differences between the edge and far distances into the interior were at scales too great to detect threshold values.

We found greater patch size to be positively correlated with the brood parasitism rate. We suggest a few reasonable explanations. It may be that larger patches are more attractive to cowbirds because of a greater potential number of hosts. Cowbirds abundance is positively correlated with host densities (Robinson et al. 1995, Tewksbury et al. 1998, Tewksbury et al. 1999). Larger patches may contain more potential nest sites. Another rationale to consider is the possibility that a greater number of host species that the cowbird favors may be more abundant in the larger patches. An additional consideration is that the larger patches may have habitat characteristics that the cowbird prefers, such as more abundant perch sites. Burhans and Thompson (1999) offered a similar suggestion when they hypothesized that brood parasitism levels would be higher for nests closer to greater numbers of trees because the trees offer nest-searching perches for the cowbird.

The finding that nests in larger patches may be more susceptible to parasitism may not necessarily mean that building a nest in a larger patch is potentially detrimental to

nesting. We found that nests further into the interior, in larger boxelders, and built higher up were less apt to be parasitized. Although the overall odds for parasitism are greater in larger patches, a larger patch will have more core area. More core area provides more habitat further from the edge and thus reduces the odds of brood parasitism. The results at first inspection seem contradictory: larger patches experience greater parasitism rates but have more core area and offer habitat less susceptible to parasitism. It may be that the larger patches are attractive to cowbirds, but that parasitism activities are concentrated near the edge. Gates and Giffen (1991) reported a higher density of cowbirds near the stream edge where there was a high density of breeding birds. Brittingham and Temple (1983) found that parasitism declined as the amount of open habitat around the nest increased. Tewksbury et al. (1998) found that parasitism declined with an increasing amount of forest cover.

Larger patches support multi-layered, heterogeneous canopies and might provide for more successful nesting and survival overall. Higher host densities could be an indication of more quality habitat. There are a greater number of potential nest sites in patches with higher foliage density and greater canopy cover in the area surrounding a nest may offer better concealment and thus offer a lower probability of predation (Martin and Roper 1988). In the same study on yellow-breasted chats mentioned above, Burhans and Thompson (1999) found the loss to parasitism in larger patches was balanced by greater nesting success, as the mean number of young fledged was equal in large and small patches. Paton (1994) in a review of research, reports that there was a positive relationship between nest success and patch size in 8 of 8 studies. Sedgwick and Knopf (1992) found that willow flycatchers were selecting sites with larger patches of willows and Knopf and Sedgwick (1992) found similar results for yellow warblers, suggesting the birds were selecting nest sites based on greater concealment.

#### **PRESENCE OF LIVESTOCK**

Cowbirds associate with cattle, and there is evidence that the greater the distance from a nest to active grazing reduces the odds of the nest being parasitized (Goguen and Mathews 2000, Kostecke et al. 2003). The results from our study do not support this



relationship. Similar conclusions come from other studies in New Mexico. Tisdale-Hein and Knight (2003) found evidence that the presence of cattle did not influence cowbird abundance on the Middle Rio Grande, New Mexico. They compared densities of cowbirds in riparian sites with and without cattle (within commuting distance of grazing), and did not find any differences in cowbird or female cowbird densities between the sites. Sechrist and Ahlers (2003) tracked the movements of cowbirds at two riparian sites on the Rio Grande, one grazed and the other ungrazed. Cowbirds at both sites had small home ranges and commute distances did not differ between sites. They found that cowbirds remained in areas with concentrated host densities, probably because southwestern riparian areas provide abundant food as well as hosts. They suggest that the exclusion of livestock from riparian habitat might have only limited efficiency in reducing parasitism rates.

#### **MANAGEMENT IMPLICATIONS**

Although grazing has been identified as a causal factor for the decline and endangerment of the southwestern willow flycatcher (USFWS 2002), we found no significant negative impact of grazing on brood parasitism of the Willow flycatcher in this system. There is still much to be learned about the relationship between population viability and brood parasitism but most recent literature on the flycatcher emphasize caution before managing cowbirds to benefit willow flycatcher populations and that any actions should first be evaluated on a site-specific basis (Sedgwick 2000, USFWS 2002, Rothstein et al. 2003, Sferra et al. 2003).

Cowbird trapping is commonly used as a management tool to increase or stabilize host populations. Cowbird trapping has been shown to have reduced the rate of brood parasitism for many avian species including song sparrows (Smith et al. 2002, Smith et al. 2003), black-capped vireos (Eckrich et al. 1999) and the southwestern willow flycatcher (Whitfield et al. 1999). However, for the flycatcher there is no evidence that trapping activities have increased population size or even stabilized declines (Winter and McKelvey 1999, Sedgwick 2000, Rothstein et al. 2003). There are a number of factors to consider when considering a cowbird management program. First, while brood

parasitism does occur on the Gila, there is no evidence that it affects the health of the flycatcher population. Second, although trapping may reduce local parasitism rates on a per-nest basis, evidence from other flycatcher sites and from other species indicates that trapping does not boost population levels or reverse population declines. Third, cowbird trapping is extremely costly in terms of money and labor (Rothstein et al. 2003); those resources would be better and more effectively used for habitat restoration and maintenance. Finally, cowbird trapping may have unanticipated and unwelcome side effects. Trapping uses the natural flocking behavior of cowbirds to lure free-ranging birds in to traps containing captive birds. Where cowbirds occur at relatively low densities (as on the Gila), traps may concentrate cowbirds around trap sites, thereby elevating parasitism rates in those areas beyond what might have occurred in the absence of trapping. This phenomenon may have caused the short-lived increase in parasitism recorded at Roosevelt Lake, AZ, in the first several years after trapping began there. Also, reductions in parasitism on all host species may boost populations of preferred cowbird hosts (yellow warbler, yellow-breasted chat), which may act as competitors of the willow flycatcher (Rothstein et al. 2003).

The main cause for the decline of the willow flycatcher is loss and alteration of riparian habitat in the Southwest (USFWS 2002). Recent literature discussing effects of brood parasitism advise that habitat health is a greater concern than cowbird management (Sedgwick 2000, Rothstein et al. 2003). The results of this study have shown that habitat does influence the rate of brood parasitism for the willow flycatcher. Core riparian areas on the Gila River may be less subject to the effects of brood parasitism, especially when larger boxelder are used as nest substrate. Nest heights and tree heights were significantly greater for nests that were not parasitized when boxelder was used as substrate. When willow and cottonwood were used, the nest height and tree heights were lower for nests that were not parasitized. This indicates that healthy, young willows and larger mature boxelders are prime substrate for reducing the odds of brood parasitism. In light of these results, we suggest that habitat health is of paramount importance. Through restoration efforts in the Gila Bird Area and on the U-Bar Ranch, revegetation and the promotion of healthy riparian habitat have created habitat that has been colonized by

breeding flycatchers (See Boucher et al. 2003). Grazing during the non-growing season has been shown to have minimal negative effects on riparian health (Kauffman and Krueger 1984, Knopf et al. 1988, Sedgwick and Knopf 1991) but grazing in the riparian zone during the growing season can have a negative effect on riparian health (Kauffman and Krueger 1984, Sedgwick and Knopf 1991). Grazing limited to the non-growing season may be most likely to promote natural regeneration and healthy habitat.

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## Appendix: Tables

Table 1. Brood parasitism rate by year and patch.

PATCH	1997		1998		1999		2000		2001		2002		2003		Total	
	Mean	N	Mean	N	Mean	N	Mean	N	Mean	N	Mean	N	Mean	N	Mean	N
Bennett									33.3	6	16.7	18	17.6	34	19.0	58
Beaver Pond	0.0	3	37.5	8	0.0	3	0.0	2	25.0	4	25.0	4	25.0	4	21.4	28
Cooper			0.0	1			0.0	1							0.0	2
<b>Ft.W.Ditch</b>	25.0	4	50.0	4	0.0	6	0.0	1							20.0	15
<b>Gila Bird Area</b>			0.0	5			0.0	3	100.0	1	0.0	1			10.0	10
NE1	0.0	3									50.0	2			50.0	2
NE2	0.0	1	50.0	2					66.7	3	40.0	5			38.5	13
NE4	0.0	1													0.0	1
NE3B			0.0		100.0	1					100.0	2			100.0	3
NE4			0.0	4	50.0	2	0.0	3	25.0	4	0.0	3	0.0	2	10.5	19
NE5					100.0	1			75.0	4	80.0	5	0.0	2	66.7	12
NE6													0.0	1	0.0	1
NW1	0.0	1					0.0	1	0.0	4	0.0	4	14.3	7	5.9	17
NW3			0.0	2			0.0	1	0.0	1	0.0	2	0.0	2	0.0	8
NW4	0.0	6	16.7	12	0.0	6	25.0	8	0.0	6	27.3	11	0.0	6	12.7	55
NW5					0.0	1	0.0	1	0.0	1					0.0	3
NW Stringer	0.0	1	100.0	1	0.0	2	50.0	2							33.3	6
SE0													100.0	1	100.0	1
SE1	18.8	16	47.1	17	27.3	11	15.4	13	22.2	9	28.6	14	36.4	11	28.6	91
SE2	0.0	2	0.0				0.0	4	0.0	12	25.0	4	50.0	4	11.5	26
SE3	0.0	2			0.0	1			50.0	2	0.0	3	25.0	4	16.7	12
SE4	0.0	1	0.0	2	0.0	3	33.3	3	0.0	2	0.0	1	50.0	2	14.3	14
SEA	100.0	2	100.0	1											100.0	3
SW1	0.0	3	33.3	3	0.0	2	0.0	2			0.0	1	100.0	2	23.1	13
SW2			0.0	2	0.0	1	0.0	3	0.0	7	25.0	4	33.3	3	10.0	20
SW3	0.0	2	50.0	2	0.0	2	0.0	3	0.0	2			0.0	3	7.1	14
SW4							0.0	1	0.0	2	0.0	1	0.0	1	0.0	5
SW Stringer	0.0	6	0.0	1	33.3	3					0.0	2	0.0	3	6.7	15
theNatureConserv			66.7	3					0.0	2					40.0	5
<b>Total</b>	<b>11.1</b>	<b>54</b>	<b>31.4</b>	<b>70.0</b>	<b>15.6</b>	<b>45</b>	<b>11.5</b>	<b>52</b>	<b>18.1</b>	<b>72</b>	<b>25.3</b>	<b>87</b>	<b>21.7</b>	<b>92</b>	<b>20.3</b>	<b>472</b>



**Table 2.** Chi-squared tests results. Differences between the observed rates of brood parasitism in each patch and the expected rates were compared. Observed and expected rates are the number of nests parasitized (BHCO\_Y) and not parasitized (BHCO\_N). Northeast 1, Southeast 1, and Northeast 5 had significantly higher rates than expected.

PATCH	Observed			Expected		P-Value
	BHCO_Y	BHCO_N	SUM	BHCO_Y	BHCO_N	
Bennett	11	47	58	11.45	46.55	0.88183
Beaver Pond Stringer	6	22	28	5.53	22.47	0.82265
Cooper Property	0	2	2	0.39	1.61	0.48305
Fort West Ditch	3	12	15	2.96	12.04	0.98001
Gila Bird Area	1	9	10	1.97	8.03	0.43895
Northeast 1	5	8	13	2.57	10.43	0.08997
Northeast 4	2	17	19	3.75	15.25	0.31287
Northeast 5	8	4	12	2.37	9.63	0.00004
Northwest 1	1	16	17	3.36	13.64	0.15110
Northwest 3	0	8	8	1.58	6.42	0.16067
Northwest 4	7	48	55	10.86	44.14	0.19121
Northwest 5	0	3	3	0.59	2.41	0.39031
Northwest Stringer	2	4	6	1.18	4.82	0.40297
Southeast 1	30	66	96	18.95	77.05	0.00462
Southeast 2	3	23	26	5.13	20.87	0.29330
Southeast 3	2	10	12	2.37	9.63	0.78895
Southeast 4	2	12	14	2.76	11.24	0.60800
Southwest 1	3	10	13	2.57	10.43	0.76263
Southwest 2	2	18	20	3.95	16.05	0.27371
Southwest 3	1	13	14	2.76	11.24	0.23628
Southwest 4	0	5	5	0.99	4.01	0.26742
Southwest Stringer	1	14	15	2.96	12.04	0.20329
The Nature Conservancy	2	3	5	0.99	4.01	0.25514

**Table 3.** Microhabitat variables. Differences in means between parasitized nests (BHCO\_Y) and non-parasitized nests (BHCO\_N) for each tree species.

	Mean			Mean			Mean			Mean		
	Nest Height		F-stat	Tree Height		F-stat	DBH		F-stat	Height Proportion		F-stat
	BHCO_Y	BHCO_N		BHCO_Y	BHCO_N		BHCO_Y	BHCO_N		BHCO_Y	BHCO_N	
Boxelder	6.1	8.5	0.000	11.7	14.0	0.005	17.4	26.1	0.002	0.543	0.611	0.044
Arizona Alder	2.6	6.0	0.013	5.3	10.9	0.134	3.4	12.3	0.035	0.575	0.547	0.888
Seep Willow	2.4	1.9	0.576	4.3	2.8	0.024	2.6	1.9	0.458	0.540	0.676	0.531
Fremont Cottonwood	4.0	5.9	0.678	16.0	10.1	0.475	15.0	11.4	0.773	0.250	0.599	0.126
Gooding's Willow	3.5	3.2	0.544	8.0	6.9	0.263	8.7	7.2	0.313	0.485	0.527	0.406
Coyote Willow	2.1	2.5	0.302	3.6	3.9	0.634	1.8	2.2	0.528	0.590	0.657	0.376
Tamarisk	2.5	2.8	0.630	3.4	7.5	0.161	5.4	8.2	0.440	0.7091	0.4494	0.127
All Species	4.7	6.9	0.000	9.4	11.8	0.001	12.8	20.5	0.000	0.551	0.593	0.111

**Table 4.** Logistic Coefficient (B), Standard Error (SE), Likelihood-ratio significance, and Odds Ratio (Y) for Univariate Logistic Regression.

Variable	$\beta$	SE	Likelihood-ratio	
			Significance	Y
Nest Height (m)	-0.194	0.047	0.000	0.824
Trunk Diameter at Breast Height (cm)	-0.046	0.013	0.000	0.955
Patch Area (ha)	0.162	0.047	0.001	1.176
Tree Height (m)	-0.088	0.027	0.001	0.916
Proportional Height of Nest	-2.157	0.780	0.005	0.116
Distance to Stagnant Water (m)	-0.002	0.001	0.028	0.998
Distance to Edge (m)	-0.019	0.010	0.057	0.981
Distance to Grazing (m)	-0.001	0.001	0.276	0.999
Distance to Floodplain (m)	0.002	0.003	0.355	1.002

**Table 5.** Logistic Coefficient (B), Standard Error (SE), and Odds Ratio (Y) for variables in parasitization model.

Variable	$\beta$	SE	Significance	Y
Nest Height (m)	-0.157	0.049	0.001	0.85
Distance to Edge of Patch (m)	-0.021	0.012	0.065	0.98
Patch Area (ha)	0.134	0.052	0.010	1.14
Constant	-1.064	0.499	0.033	0.35